

LECTURE II

THE MECHANISM OF ADAPTATION

THE wonderful adaptations of organisms to their environments, of structures to habits, of responses to needs, of means to ends, have ever been and still are the greatest problems of biology. From the time of the early Greek philosophers to the present day, the mystery of life has centered to a large extent in this great problem of how organisms came to be so marvelously adapted, in structures and functions, for their preservation and welfare. Aristotle maintained that the essence of a living thing is its fitness, and after centuries of observation, experiment, and theorizing we must still say that one of the most mysterious and inexplicable phenomena in nature is the capacity of the lowest plants and animals, as well as of the highest, to respond to external conditions and stimuli in a useful and an apparently intelligent and purposive way, although it is certain that conscious intelligence and purpose are not usually involved.

How have lowly organisms learned to utilize processes of chemistry and physics so subtle in character that intelligent man after centuries of civilization has come only to the place where he can appreciate these processes but cannot duplicate them? How have those units of living matter, the cells, come to have complex teleological mechanisms for assimilation, growth, and division, for secretion, contraction, and sensation? How can we explain the origin of multitudes of inheritance units, their location in the chromosomes, the wonderful mechanism of mitosis for the precise division and distribution of these chromosomes to all

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the cells of the body; and how explain the union of homologous maternal and paternal chromosomes in synapsis and their unique method of separation in the reduction division, upon which processes the phenomena of Mendelian inheritance depend? How is it possible to explain the adaptive mechanisms of the egg and sperm and of the processes of fertilization? How can we explain the teleological character of embryonic development, in which the end is apparently in view from the beginning? How is it possible to account for the adaptive tropisms, reactions, and instincts of animals, the complicated but delicately adjusted relationship between different individuals and species, their ingenious means of defense and offense and the surprising efficiency of the living machine? Finally, is it possible to find any natural and causal explanation of the adaptations of individuals to conditions which neither they nor their ancestors have ever before experienced?

The list of such fitnesses is well-nigh endless, and the question of their origin forms one of the most striking and fundamental problems of biology. It may be necessary for the biologist to disregard this problem for the present because he cannot deal with it, but he should never forget that it is a real problem and challenges scientific explanation. This subject is undoubtedly a dangerous one for the scientist, full of pitfalls for the unwary and with many alluring calls to metaphysical speculation; but it lies in the background of every biological problem. As Professor W. K. Brooks taught, "Life is response to the order of nature," and it is the element of useful and apparently purposive response which more than anything else distinguishes the living from the lifeless, and separates the methods and results of biology from those of chemistry and physics.

Innumerable attempts have been made by philosophers

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and biologists to find an explanation for adaptation. One need only enumerate the "supernatural design" of theologians, the "perfecting principle" of Aristotle and Nägeli, the "indwelling soul" of Plato and Bruno, the "active teleological principle" of Kant, the "unconscious purpose" of Hartmann, the "vital activity" or "vitalism" of Bunge, Wolff, and Virchow, the "will" of Schopenhauer, the "élan vital" of Bergson, the "entelechy" of Driesch, the "archæsthetism" of Cope, the "desire" or "need" of Erasmus Darwin and Lamarck, and finally Charles Darwin's "natural selection," to indicate over what a wide field these attempted explanations have ranged. All of these proposed explanations may be classified as natural or supernatural, or more accurately as mechanistic or vitalistic. The former presuppose only natural forces and processes in the regular sequence of cause and effect; the latter assume that some form of will or purpose is present as an uncaused cause which lies outside the field of scientific inquiry.

If for the present we pass over those views which attempt no casual explanation, but merely restate the mystery in terms of supernatural design, perfecting principles, or entelechies, and those which find the causes of adaptations in unknown laws of variation or of physiological response, there remain two attempted explanations of organic fitness which may be known by the general terms of Lamarckism and Darwinism, though at present neither of these systems represents accurately the views of the man whose name it bears.

1. *Lamarckism*

Lamarckism attempts to explain racial adaptations as the result of the inheritance of individual or acquired adaptations; it is assumed that the beneficial responses which are called forth in individuals by external stimuli are handed

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on to later generations by heredity, and in this way racial adaptations are supposed to have originated. Thus all racial or inherent adaptations are held to have come from individual or acquired ones. The increased pigmentation of the skin of one who is exposed to tropical light is said to be inherited by his children, and so a dark-skinned race arises; the stretching of the neck and legs of any animal that browses on trees is supposed to be inherited, and so the giraffe was evolved. Such an explanation is so simple and plausible that it has been widely accepted. Unfortunately for this attractive explanation, there is no evidence that it is true. The evidences in favor of the inheritance of any somatic modification are very unsatisfactory, and when it comes to the inheritance of acquired *adaptations*, critical evidence is lacking altogether. For years evidences of such inheritance have been earnestly sought, but no such confirmations have been found as would certainly have been the case if this kind of inheritance were at all common.

On the other hand, there seems to be no reasonable escape from the postulate that modifications of the germplasm are produced by environmental influences. The germ-cells, and more especially the chromosomes and genes, are well protected from almost every change in the external environment, but there is an internal environment of body fluids and of cytoplasmic and nuclear substances which comes into much more intimate contact with the germplasm, and it seems necessary to assume that certain changes in this internal environment may cause changes in the germplasm itself. Some experimental evidence, especially that of Guyer and Smith on inherited eye-defects in rabbits, favors this view.

However, such environmental modifications of the germplasm are not generally adaptive, and the beneficial charac-

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ter of germinal modifications must be explained in some other way. The assumption that individually acquired adaptations of parents are directly inherited by their offspring and thus become racial is not supported by any critical evidence.

Furthermore, there are many adaptations that benefit the species at the expense of the individual. For example, in many instances the reproductive instincts lead directly to the death of the individuals concerned; every male bee, every male and female salmon, goes to its certain death in perpetuating the species. Such adaptations that are for the good of the race but lead to the death or injury of the individual cannot be explained by the Lamarckian theory that racial adaptations are merely individual adaptations that have become hereditary.

Samuel Butler, Bergson, Bernard Shaw, and many others maintain that the evolution of adaptations cannot be explained except on the basis of Lamarckism. Herbert Spencer said, "If there is no inheritance of acquired characters, there is no evolution"; but it is evident that Spencer did not define with sufficient clearness what he meant by "acquired characters." In one sense random mutations are acquired characters, but they are not somatic modifications due to use or disuse. Sumner says, "The imperative demand for *directed* germinal variations can be met only by assuming the inheritance of acquired characters. . . . Adaptations have come about not because of their harmlessness but because of their utility." But in spite of theoretical necessities, it is a fact that mutations occur in many directions; they are multifarious, and in their origin they do not seem to be directed any more than "the course that the wind blows." The directing comes after their appearance and through the elimination of the less fit.

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It is a mistake to suppose that Lamarckism explains the real origin of adaptations; it maintains that individually acquired adaptations are inherited and thus become racial, but it attempts no other explanation of the origin of individual adaptations than is to be found in "desire," "need," or "will." The beneficial character of the response of an organism to changes in its environment and to use, disuse, and needs remains as much of a mystery as ever. Lamarckians who have attempted to explain acquired adaptations have generally appealed to some mysterious principle, such as unconscious purpose, entelechy, *élan vital*, or vitalism as contrasted with mechanism; thus the search for the causes of acquired adaptations is removed from the field of scientific inquiry. Lamarckism is thus fundamentally non-mechanistic, and it is not surprising that vitalists and obscurantists generally should favor the Lamarckian philosophy.

In order to explain racial adaptations, Lamarckism begins with the unproved and discredited assumption that individually acquired adaptations are inherited, and in attempting to explain the origin of individual adaptations it ends in a fog of obscurantism or in a bog of mysticism.

2. Darwinism

Darwinism, on the other hand, rejects the possibility of the inheritance of such individual or acquired adaptations and maintains that there is no *genetic* connection between racial and individual fitness. It holds that all racial adaptations are due to (1) multifarious variations (mutations) among offspring and (2) the elimination by natural selection of those that are poorly adapted. It will be seen that all adaptations that are for the good of the species rather than of the individual admit of no other natural explanation, for such adaptations could not have arisen from

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the beneficial responses of individuals, as Lamarckism assumes, since they benefit the species at the expense of the individual.

The probabilities are distinctly favorable to these two fundamental propositions of Darwinism. We know that mutations occur in many directions, and that most of them are not beneficial. We know that the more injurious they are the earlier the individuals possessing them are eliminated. There is an immense elimination of germ-cells; among mammals not one spermatozoon among billions ever fertilizes an egg, and not one egg in thousands matures and is fertilized; and while it must often happen that the fittest perish along with the most unfit, still it is highly probable that on the whole the germ-cells that are fertilized and begin to develop are among the fitter. There is a large elimination of embryos and larvæ; among many animals thousands perish for every one that survives; and again, it is most probable that on the whole and in spite of individual exceptions it is the fitter that survive. Many young and sexually immature individuals die for every one that arrives at sexual maturity, and here also the survivors are in general the fitter. There is thus an immense elimination of individuals in every generation before they reach the period of reproduction, and most of this elimination is wholly unseen and unknown by the casual observer of nature.

On the whole, much of this elimination is discriminative; there is universal elimination of the most unfit and, in general, survival of the better fitted. It is true that in many catastrophes destruction is wholly indiscriminate and the fit and unfit perish together. Even in the more usual forms of elimination, it does not happen that in every generation and in every individual instance the fitter survive and the less fit perish; but if this happens in the majority of cases, it

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will in the course of time bring about the diminution of unfitness and the general prevalence of fitness. Darwin showed in masterly manner that the greater elimination of unfit individuals in each generation and the more general preservation of better fitted ones would gradually improve the standard of fitness until finally such exquisite adaptations as are found in the eye, for example, might be reached. This seems to me to be the crowning glory of Darwin's great theory; it is not so much its species-forming power which impresses one as its ability to explain on simple and natural principles very many of the wonderful adaptations of the living world.

3. Mutation Theory

The mutation theory has to a certain extent changed our point of view regarding adaptations as it has also regarding species formation. Neither of these phases of evolution can any longer be regarded as the result of minute variations which persist and replace ancestral forms, if they are infinitesimally better adapted, but mutations may represent relatively large changes both in form and usefulness. They occur in many directions and are usually non-adaptive and are frequently positively injurious. The latter are quickly eliminated in a state of nature, but indifferent mutations may persist, and it is no longer necessary to assume, as older Darwinians did, that every structure of an organism is of some benefit to its possessor; on the contrary, it appeared without reference to its usefulness or its uselessness, and it persists only if it is not injurious.

Preadaptations.—In applying the mutation theory to the explanation of adaptations, Cuénot has proposed a modification of the Darwinian theory which he calls "preadaptation." Mutations which are injurious or indifferent in the

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environment in which they arise may be well fitted for some other environment and will persist if they can find that other environment. Thus white insects or spiders, which probably originally appeared as sudden mutations, are badly fitted to live on a dark object, since they are so conspicuous; but they are well fitted to live on a white background—for example, white flowers. Their white color was not acquired by a long and slow process in order to fit them to live on white flowers, but white mutants appeared suddenly and then found, by a process of trial and error or by natural selection, an environment for which they were suited. Loeb has shown that fish with degenerate eyes may be produced by hybridizing two species with normal eyes or by keeping normally fertilized eggs at a temperature of 2° C. for several hours after fertilization. Such fish were not slowly adapted to life in caves or dark places, but, since they stand a very unequal chance of survival in competition with seeing forms in the light and probably an equal chance in the dark, they can survive only in dark places. Thus the blind fauna of caves was not made for life in the dark, but blind or nearly blind animals found in caves an unoccupied place in nature where seeing did not offer any advantage. In short, the adaptation was present before its fitness was discovered by its possessor; the environment did not make the adaptation but merely revealed it. This is, as I understand it, the same conception which has been called by ZurStrassen "organized seeking."

Cuénot cites as instances of such preadaptations the following cases among many others: Any beneficial change of food or habitat, such as the turning of certain butterflies or moths from particular species of flowers which they ordinarily frequent to other species; or the newly acquired habits of the ground parrot (*Nestor notabilis*) of New

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Zealand, which was originally an insect-eating and fruit-eating bird, but which has become more or less carnivorous since the introduction of sheep into that country; it was evidently well fitted, or preadapted, for this new kind of food even before the food appeared. All such fitnesses were developed without regard to their later use; they are therefore preadaptations.

Cuénot further points out that such preadaptations, or fortuitous conjunctions of favorable environment and characters preadapted to this environment, have been an important factor in progressive evolution. For example, the appearance of several great classes of the animal kingdom has followed the occupation of a place, either unoccupied or peopled by an inferior group not able to resist the invasion. Thus shallow-water fishes have given birth by mutation to amphibians capable of living in a merely humid environment, thanks to their aërial respiration and walking limbs. From these issued reptiles which occupied dry regions; their hard skin, digits armed with claws, internal fecundation and large eggs, capable of direct development, permitting the omission of an aquatic stage, were preadaptations necessary to this change of habitat. Birds, derived from reptiles, peopled the unoccupied realms of the air owing to their preadaptations for flight. Mammals derived from primitive reptiles were able to replace these because of their intra-uterine development, maternal protection of the young and constant temperature. Man has been able to prevail over preceding forms because of his superior brain—all these fitnesses being preadaptations.

This theory of preadaptation is evidently a modification and extension of the Darwinian doctrine to the origin of adaptations, as the mutation theory is an extension of that doctrine to species formation; it is merely a variant on the theme of natural selection.

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4. Individual Adaptations

But while Darwinism as thus expanded is able to explain the origin of racial or inherited adaptations, it does not, as ordinarily understood, succeed in explaining the numerous and equally remarkable individual adaptations of organisms any more than Lamarckism does; indeed, some of these individual adaptations have been held by several recent writers to be absolutely fatal to both of these theories. For example, it has been found that if the lens of the eye of a newt is removed it will be regenerated perfectly within a few weeks. Now it may be granted that such an injury as this, involving as it does a very delicate surgical operation, never took place in nature; newts may have had their heads bitten off from time immemorial, but they never had the lens removed from the eye except in an experiment directed by human intelligence; and yet Darwinism in its original form can explain this regeneration only by supposing that the loss of the lens has taken place so frequently among the ancestors of present-day newts that they have become perfectly adapted to this injury by the more frequent survival of those which were inherently capable of regenerating the lens.

Again, the eggs, embryos, or adults of many animals may be cut or broken into fragments or otherwise injured in such ways as could never have occurred in nature, and yet these fragments will, in many cases, give rise to perfect animals "as if the pattern of the whole existed in every part." This power of regeneration cannot be the result of past experience, since there is no constant correlation between its occurrence and the liability to injury. Other contingent, individual adaptations that are most difficult to explain are found in the acclimatization of certain organisms to extraordinarily high temperatures and in the toleration

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that may be developed for violent poisons; such acclimatization or toleration cannot be due to the elimination on a large scale of organisms that cannot become adapted, since in well-conducted experiments few if any of the individuals perish. In the case of bacterial toxins or snake venom, the manner in which tolerance to the poison is brought about is better understood than in the case of other poisons. It is known that the body that is poisoned forms various antibodies as antidotes to these poisons, and for every toxin, or at least for every toxalbumin, its particular anti-body; but why a particular toxin causes the formation of its one appropriate antitoxin is a mystery. Many of these toxins are of such a sort that it is perfectly certain that the immediate ancestors of the individuals poisoned could never have had experience with them, as, for example, in the case of guinea-pigs inoculated with cobra venom; and yet the response is as perfect as it could be if it had been due to long experience. Many other similar cases might be cited, but these are enough to indicate how difficult it is to find a natural explanation for these individual, contingent adaptations. Indeed, it may be said that the apparently intelligent and purposive response of an organism to a stimulus or environment which it or its ancestors have never experienced before is one of the most important and mysterious problems of biology.

Both Lamarckism and Darwinism hold that *racial* adaptations are due to experience; Lamarckism, that they are the directly inherited effects of individual experience; Darwinism, that they are the indirect results of ancestral experience operating through the presentation of many variations to the action of natural selection and the survival of the better adapted. Neither of these theories explains sudden adaptations of *individuals* to conditions never experienced before.

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It has sometimes been said that while racial adaptations are due to natural selection, individual adaptations are due to the "plasticity" of the organism; but this is merely seeking refuge in a name. Plasticity is only passivity and is no explanation at all. It has also been suggested that individual adaptations are problems of development rather than of evolution, of physiology rather than of phylogeny. But this distinction also is nominal rather than real, for evolution is only one form of development, and phylogeny no less than ontogeny must be based on physiological processes. It is true that individual adaptations are things with which we can deal directly by experimental methods, whereas racial adaptations were established in the more or less distant past and are not readily submitted to experimental tests. Therefore we ought to know more about the causes of individual adaptations than of racial ones, but hitherto attention has been focussed largely upon the latter and relatively little study has been given to the former. One of the greatest needs of biology is for more detailed and accurate information regarding individual adaptations; we must know exactly what happens in each case—the physiology of the response irrespective of its usefulness—and then perhaps the latter may find an explanation.

Many of these physiological processes are in a certain balance with one another or with the environment, and when this balance is disturbed there is a compensatory regulation. For example, a muscle that is neither increasing nor decreasing in size receives a certain amount of blood; increased use of this muscle is balanced by an increased flow of blood, and decreased use leads to a decrease in the blood supply; correspondingly, the muscle increases or decreases in size. Similarly, if one kidney is removed the one that remains has to perform the functions of two, and it receives more blood

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and grows in size. If much blood is lost in hemorrhage the activity of the blood-forming organs is increased, and they send more corpuscles and plasma into the circulation; for there is a certain equilibrium between the activity of the blood-forming organs and the quantity of blood in circulation. If white corpuscles are destroyed by x-rays the lymphoid tissues are stimulated to send an excess of leucocytes into the blood, to compensate this deficiency.

This tendency to equilibrium is probably one of the most important physiological processes in the regulations and adaptations of organisms. A similar tendency is found in the inorganic world; when the osmotic pressure between two fluids separated by a permeable membrane is unequal, equilibrium is automatically restored; when the gas tension differs on two sides of a permeable membrane, diffusion occurs through the membrane until the tension is equal on both sides; when the oxygen or carbon-dioxide tension in the blood differs from that in the tissues or in the lungs, there is an exchange of gases until equilibrium is reached; a chemical reaction proceeds in the direction of equilibrium, and if an excess of products is formed in one direction the reaction may sometimes reverse and go in the other direction until equilibrium is restored. Such cases seem to be analogous with the compensatory regulations of organisms, but the balance between one physiological process and another or between the organism and the environment is not only vastly more complex than these inorganic equilibria, it is self-preservative and useful; and it is this quality of usefulness or fitness for which we are seeking an explanation.

It is possible that some of these individual adaptations belong to the fundamental and original properties of living things and as such are not to be explained by any theory of evolution; for it must not be forgotten that organic evolu-

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tion is a theory of transmutation which undertakes to explain the diversities which exist in the living world, but not the original properties of life. It undertakes to explain the various forms of adaptation found among organisms, but not organic adaptability. It may be that regulation or regeneration is one of the fundamental physiological properties of living things, and that it belongs in the same category with assimilation, growth, metabolism, reproduction, and irritability—properties which are found in the lowest organisms as well as the highest, and which can therefore be left out of the list of things which organic evolution may reasonably be expected to explain. But this would certainly not apply to peculiar, individual adaptations such as have been named. The origin of these must be explained no less than the origin of particular racial adaptations. Moreover, it is incredible that things so much alike as racial and individual adaptations should be due to wholly different causes.

It seems, therefore, that while natural selection is a fairly satisfactory explanation of racial adaptations, it does not, in the form proposed by Darwin, furnish a satisfactory explanation of individual adaptations, and this has led several biologists, notably Wolff and Driesch, to the conclusion that Darwinism "fails all along the line," while many who are not biologists have hailed with joy what they regard as the "death of Darwinism." But this conclusion is certainly unwarranted and extreme. There are many racial adaptations, as we have seen, which are beautifully explained by the Darwinian theory, and it is certainly premature to abandon hope of explaining individual adaptations by a similar principle.

5. Intra-personal Selection

Weismann recognized that natural selection as set forth by Darwin was not a satisfactory explanation of all phe-

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nomena of evolution, and especially of the degeneration and disappearance of useless parts and the concordant modification of numerous parts of the organism. In order to explain these he proposed to extend the principle of natural selection from individuals or persons ("personal selection" or "Darwinism" in the strict sense) to organs and tissues ("histonal selection" of Roux), and even to germinal units such as determinants and biophores ("germinal selection"). This hypothesis as originally proposed was open to many and serious objections. It is impossible to hold with Weismann that there is a struggle between germinal elements for food, and that the weaker ones are starved and eliminated in this struggle; but we are on safe ground when we affirm that natural selection is operative at every stage in development from the earliest steps in the formation of the germ-cells up to the adult condition. Not even the most radical critic of Darwinism doubts that animals which cannot live die. No one doubts that this is true also of individual cells as well as of persons. What reason is there to suspect that it is not also true of parts of cells, such as plastids, nuclei, chromosomes, chromomeres, and even genes? We know that many young forms perish before reaching maturity, that numerous organisms never develop beyond embryonic stages, that multitudes of germ-cells perish, and that, in general, elimination is much more severe in the earlier than in the later stages of ontogeny. We know that in the life of higher organisms many kinds of cells are continually dying and being replaced by others; so far as epithelial, glandular, and blood cells are concerned, we may say with St. Paul, "We die daily." The death of cells is frequently selective; for example, it is said by medical authorities that the leucocytes or white blood cells are destroyed in large numbers by the influenza germ, thus opening the way to infection by

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many germs, especially those affecting the respiratory tract. It is known also that x-rays kill certain cells, particularly the leucocytes, sooner than others. We know that it is possible to destroy parts of a cell and yet keep other parts alive for a time at least; whole chromosomes may be lost and yet the cell be capable of continued life and division. What reason is there for supposing that the same may not be true of the units of which chromosomes are composed, and even of the genes themselves? If this should be true, the elimination of the unfit may take place at any stage in the ontogeny, and the least viable would be those which disappear earliest and leave fewest traces. The greatest misfits in the world never become visible to the naked eye, for they never begin to develop. In this way doubtless many mutations are eliminated before they ever come to light, and so modifications which are disharmonious disappear almost as soon as they occur.

Recent work of Morgan and his pupils shows that there are inheritance factors or genes which are transmitted in Mendelian fashion and which cause death either before development begins or at some time during that process. These "lethal factors" bring about the complete elimination of certain genotypes, so that natural selection may be said to begin in such cases with the genes themselves. But it may be objected that such selection is not necessarily adaptive, that it does not represent the survival of the fittest, since these non-viable genotypes might have given rise to phenotypes which were highly adapted to conditions of life if only they could have lived; but it must not be forgotten that in order to leave offspring organisms must live, and that fitness to survive must be found not merely in adult stages but in every stage leading up to the adult. Those individuals that leave offspring must be fit *at all stages of development*

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to persist in the conditions in which they are found; those that leave no offspring may be fit to live, but they are unfit for the perpetuation of the species, and those that are incapable of beginning development are least fit of all.

6. *Trial and Error*

Such elimination of persons or cells or genes would not, however, explain individual or contingent adaptations, which are really only beneficial responses to environmental stimuli in which no elimination of individuals occurs. It seems to me that many, perhaps all, such adaptations may find a mechanistic explanation in the further extension of the selection principle to the physiological responses of organisms. Herbert Spencer explained adaptive motions on the principle of "overproduction of movements" and the persistence of those that are beneficial. Darwin suggested this method of explaining the apparently intelligent behavior of the earthworm. Lloyd Morgan applied this principle to the study of animal behavior under the designation of "trial and error." In a series of masterly works Jennings has proved that the beneficial responses shown by many lower organisms may be reduced to this simple principle of "trial and error"; in this way apparently purposive behavior which Binnet supposed to be due to the relatively complex "psychic life of micro-organisms" has been shown to be due to a few simple motor reflexes, which are repeated indefinitely until they bring the organism into a favorable environment. Many recent investigators have shown that this principle is applicable to the behavior of a large number of animals.

This principle of overproduction of movements or of "trial and error" is in reality the rejection, elimination, or cessation of unfit responses and the persistence of beneficial ones. It has hitherto been applied only to motor reactions,

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but in 1909 I suggested that it might be applicable to many other organic reactions. ZurStrassen has generalized this principle under the title "overproduction of opportunities (Gelegenheiten)." If this principle should be found applicable to physiological responses in general it would explain in equally simple manner many apparently purposive responses which are at present inexplicable. It is known, for example, that immunity to bacterial or other toxins is not acquired immediately but only after a certain lapse of time during which physiological processes are more or less disturbed; there is frequently an increase of destructive metabolism, the body temperature rises, and there are other abnormal conditions. "Fever is the process of adaptation to such toxic agencies as can be neutralized by the development of anti-bodies" (Adami and McCrea, p. 149). It is at least possible that during this period the responses to the toxin are in the nature of trial and error, that many kinds of anti-bodies are formed, and that the production of useless kinds gradually ceases while beneficial ones continue to be formed. This last might be explained as a result of the establishment of chemical equilibrium, for if many kinds of anti-bodies are formed and only one is used up in the "fixation" of a toxin, this one would continue to be formed while the other kinds would not.

If this suggested explanation of individual adaptations should prove to be true, it would mean that the living, developing, reacting organism is like a swimming *Paramecium*; it tries many paths, eliminating or ceasing to follow useless or injurious ones and persisting in the beneficial ones. Such an hypothesis implies in many cases the capacity on the part of organisms to distinguish between harmful and beneficial conditions, and this capacity is left unexplained. Since it is present, however, in living things generally, it may be

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considered to be one of the original properties of life, and our inability to explain its origin is not different from our inability to explain the origin of metabolism, reproduction, irritability, or of life itself. Thus the simple principle of overproduction and the elimination of the injurious or unfit, whether individuals, cells, or physiological responses, would offer a possible mechanical explanation of both racial and individual adaptations and of the almost universal occurrence of fitness in the living world.

There are, however, certain difficulties which such an explanation encounters, and there is always left an unexplained remainder which for the present at least is inexplicable on purely mechanical principles. One of the most serious of these difficulties is that the rate of adaptation does not appear to be proportional to the rate of overproduction and elimination, as it should be if these are the only causes of adaptation. The rate of adaptation can be measured by the rate of divergent evolution, that is, adaptations in different directions, or by the relative complexity and perfection of corresponding adaptations in two groups of approximately equal age. Measured in either of these ways, we find that the rate and degree of differentiation and adaptation are not always proportional to the amount of overproduction and elimination. The rate of reproduction and of elimination is lowest in some genera and classes in which adaptations are most varied and perfect. For example, compare the rate of reproduction and elimination in lower animals and plants with that in higher ones. If the variety or complexity of adaptations is dependent entirely upon these two factors, why do not bacteria and protozoa have the most numerous and complex adaptations of all organisms; or why do not mice greatly surpass elephants in these respects; or grasses, sequoias; or why is not

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man one of the least highly adapted of all animals? Certainly some animals and plants which have the lowest rate of reproduction and elimination have the highest types of differentiation and adaptation.

One answer to this argument is that one organism is as well adapted as another, and that there are no such differences in fitness as have been assumed. For example, an amœba may be as well adapted to its environment and needs as a man is to his. If one has reference only to the capacity to survive and leave descendants, this is certainly true. Every individual or species that persists must be well enough adapted to live and multiply. But adaptations differ greatly in *number* and *complexity* in higher and in lower organisms, just as differentiations do, and, since these adaptations have arisen in the course of evolution, those animals and plants that have the more numerous and the more complex adaptations must have had a longer course or a more rapid rate of evolution. However, the duration of evolution cannot have been longer in higher forms than in lower ones; if all organisms have had a common origin, all are equally old so far as ancestry and evolution are concerned, and if one considers only the different phyla, classes, genera, etc., it is evident that these are much older in the lower than in the higher forms.

It must therefore follow that the rate of evolution and of adaptation has been much more rapid in higher than in lower organisms in spite of the fact that in general the rate of reproduction and elimination of persons has been lowest in those forms in which adaptation has gone farthest and fastest. A possible explanation of this apparent contradiction of the Darwinian theory is found in the fact that higher organisms have more different kinds of genes as well as more differentiated cells and organs than the lower ones, and

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even if mutations of genes occurred with equal frequency in all organisms (which seems improbable), those in which the genes were most numerous and most differentiated would furnish the largest number of mutations. If this should prove true, the rate of mutation should be greatest in the most highly differentiated organisms. Incidentally, the fact that the number of mutations is not proportional to the number of germ-cells that undergo maturation and fertilization is evidence that evolution and adaptation do not depend largely upon Mendelian segregation and recombination of genes, and it also indicates that gene mutations are not limited to the period of maturation of the germ-cells.

In view of the fact, therefore, that there is in general a much greater overproduction and elimination of individuals in lower than in higher animals, it is possible to maintain the Darwinian theory only by assuming that there is a greater production and elimination of mutants in higher forms than in lower ones; if this be true, it would explain on mechanistic grounds the more numerous and more complex adaptations of higher as compared with lower organisms.

On the other hand, the more rapid evolution and adaptation of higher animals would be easily explained by Lamarckian principles. If desire and intelligence are factors in evolution, then it should follow that with increasing intelligence there should be an increasing rate of evolution and adaptation. Certainly these two—intelligence and rapidity of evolution—seem to be associated, but whether as cause and effect we cannot say. Evolution has undoubtedly led to intelligence; has intelligence in turn affected evolution?

Finally, whether the Darwinian theory, as thus expanded, is capable of explaining all the fitnesses of organisms or not, it does succeed as no other theory does in offering a casual or mechanistic explanation of very many of these wonderful

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phenomena. The development of particular structures and functions fitted to particular conditions of life, such as organs of locomotion, sensation, respiration, digestion, offense, and defense, and all the multitudes of diverse forms and ways in which organisms are fitted to carry on the fundamental properties of life amidst the most varied conditions—these adaptations we may reasonably expect a theory of evolution to explain, and it is the crowning glory of Darwin's theory that it is, on the whole, able to explain them.

In the preface to his "Vorträge über Descendenz-theorie" Weismann says: "The selection principle controls in fact all categories of life units. It does not create the primary variations, but it does determine the paths of development which these follow from beginning to end, and therewith all differentiations, all advances of organization, and finally the general course of development of organisms on our earth, for everything in the living world rests on adaptation." I have here proposed that the selection principle is also applicable to physiological reactions as well as to vital units, that it lies at the basis of behavior as well as of bodily structure, and that even instinct, intelligence, and purpose are themselves the residuum that is left after the elimination of unfit responses. The selection principle is the only causal and intelligible explanation of all forms of adaptation, and if we reject it we can turn only to non-mechanistic explanations.